THE EFFECT OF STARVATION ON THE WING DEVELOPMENT OF MICROSIPHUM DESTRUCTOR.

LOUISE H. GREGORY.

As is the case with aphids in general, the life history of *Microsiphum destructor*, the green pea-aphid, shows a definite relation to the environment. Dimorphism is common. Winged and wingless individuals appear in varying numbers at different stages in the life history, the wingless forms predominating in the early part of the reproductive history, the winged forms increasing in number toward the end of the summer. While it is generally accepted that external conditions probably control the appearance of wings, very little data has been offered as proof. For a number of years, at the suggestion of Professor Morgan, I have experimented with the effect of starvation on the production of winged forms in the families of the green pea-aphid. I am glad to express my appreciation of Professor Morgan's helpful criticisms.

In starting all experiments, a single individual, selected to produce the stock family, was isolated on a young pea plant in a small pot and covered with a lamp chimney, the top of which was covered with gauze to prevent the escape of the aphid and the confusion of families. This method of isolation was used throughout the investigation and proved most successful, the plants growing normally, sufficient air entering at the top of the chimney. From the family of the stock aphid, some young were isolated and used as control lines, others were removed daily from the plant and starved for periods of different lengths, twenty-four hours, twelve hours and eight hours. Experience proved that fewer deaths resulted if the aphids were starved eight hours daily. After the period of fasting the starved aphids were isolated and their offspring observed. As will be clear later, the effect of starvation on wing development is not apparent in the individuals starved, but in their offspring.

Table I.

Starvation Exp. I. *Control.*

Parent non-winged.
Both series from one parent.
A2 series younger.

Date 1913–14, winter. 1913–14.

No. Exp.	Hours Starved.	No. Non-winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.	No. Exp.	No. Non-winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.
A1 series	30					Starved—						*Winter*
No. 2		14	49	63		4 days—av. $7\frac{1}{2}$ h.	No. 2	31	14	45		
No. 3		6	34	40		per day—	No. 4	43	4	47		
No. 6		14	73	87			No. 6	28	23	51		
No. 7		25	61	86			No. 8	32	9	41		
No. 8		39	37	76			No. 10	41	3	44		
		—	—	—		Av. family		—	—	—		Av. family
		98	254	352	71+	70+		175	53	228	23%	45.4
A2 series	$32\frac{3}{4}$					4 days starved						
No. 2		30	0	30		av. 8.10 daily						
No. 3		27	23	50								
No. 4		34	40	74								
No. 5		23	54	77								
No. 6		24	43	67								
No. 7		35	43	78								
No. 8		16	20	36								
No. 9		25	26	51								
		—	—	—								
		214	249	463	53.8	Av. family 57						
Grand Total		312	503	815	61.1	Av. family 62						

The first experiments were carried on during the winter of 1913–1914 in the greenhouse at Columbia University (Table I.). Five young of a wingless mother were deprived of food $7\frac{1}{2}$ hours daily for four days. These (A1 series) produced a total of 352 young, 254 or 71 per cent. of which were winged. In the second series (A2) younger members of the same family, 8 aphids were starved 8 hours daily for four days. The total number of offspring in the eight families was 463, of which 249 or 53 per cent. were winged. In the control series of a total of 228 (young of five families) 23 per cent. were winged showing a difference of 48 per cent. if compared with the A1 series and of 20 per cent. with the A2 series. If the entire A series is considered as a whole, among the young of 13 families 61 per cent. were winged. Apparently the lack of food has had its effect on the second generation, none of the starved individuals developing wings.

The experiments were repeated at Woods Hole in the summer of 1915 (Table II.). Again the young of a wingless mother were used for the experiment and control. The families of seven wingless females starved 45 hours, were observed and out of a total of 188 young, one winged form only appeared. The seven families of the control series showed 3 winged individuals. Apparently the effect of fasting was overcome in some way.

Considering that the atmospheric conditions had been unusually favorable for the development of the peas, the weather having been very hot with much humidity, I concluded the food had been sufficiently rich to overcome any adverse effects of starvation, and that in order to induce the effects of starvation, it would be necessary to increase the number of starvation periods. Consequently the experiments were repeated the following summer in Princeton, Mass. (Table III.).

Five young starved 60 hours produced a total of 254 offspring, 30 per cent. of which were winged. Ten individuals forming the control series produced 514 young, of which 56, or 9.7 per cent., were winged. Here again starvation has had its effect.

Summarizing all the experiments on wingless parents, it is seen in Table III., that 25 starved individuals produced 1,257 young, 46 per cent. of which had wings: that 22 normal indi-

TABLE II.

1915. *Starvation Exp. II.* Parent non-winged. 1915. *Control.* Parent non-winged.

No. Exp.	Hours Starved.	No. Non-winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.	No. Exp.	No. Non-Winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.
A_2	45					Woods Hole	A_1					Woods Hole
(1)		37	0	37		Plants luxuriant	(1)	38	0	38		
(3)		15	0	15			(2)	71	3	74		
(4)		18	0	18			(3)	49	0	49		
(5)		32	0	32			(4)	39	0	39		
(6)		36	0	36			(5)	48	0	48		
(7)		18	0	18			(6)	34	0	34		
(10)		31	1	32			(10) ...	65	0	65		
		—	—	—				—	—	—		Av. family
		187	1	188		Av. family 26.8		344	3	282	1.	39.5

viduals produced 1,149 young, 9.7 per cent. of which were winged. The starved mothers had about three times as many winged young as the control. Since all the families were subjected to the same conditions of temperature and humidity, the variation in the results must be due to the only factor in which they differ, namely the food supply.

Temperature undoubtedly may effect the production of wings as Ewing[1] has shown in his experiments with *Aphis avenæ*. He found that by keeping the temperature constant at 65° F., he could prevent the appearance of any winged forms. At lower and higher temperatures winged forms appeared. These results might be interpreted as due *not* to the direct effect of temperature on the development of wings but on the growth of the plants or the food supply and thus indirectly affecting the metabolism of the individuals.

If the summer experiments are compared with those in the winter, it will be observed that the percentage of winged forms is less in both starved and control lines. However the percentage of increase in number of winged forms in the starved lines remains constant. In the summer as in the winter there are three times as many winged young in the starved lines as in the control. I see no reason why the temperature might not have been effective indirectly in the lessening of the wing production in both starved and control summer lines. The atmosphere of the greenhouse was practically constant, while the summer experiments were carried on out of doors and were subject to all the daily changes in temperature and moisture. The actual difference in the development of wings at any one time must have been due to the difference in food supply, temperature having no part. I believe that if aphids were starved for long periods and kept at a constant temperature of 65° F., Ewing's optimum temperature, winged individuals would appear.

Overcrowding on the plants has been suggested as a possible cause of wing development. In nature this might be true, the results however being due to a lessening of the food supply. In my experiments there was no overcrowding as the young were

[1] Ewing, H. E., "87 Generations in Parthenogenetic Pure Line of *Aphis avenæ*," BIOL. BULL., Vol. XXXI., No. 2, 1916.

TABLE III.

Starvation Exp. III. 1916 July. Parent non-winged. — *Control.* 1916 July. Parent non-winged.

No. Exp.	Hours Starved.	No. Non-winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.	No. Exp.	No. Non-winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.
	60 hrs.					Princeton, Mass.						
1		35	51	86		Alt. 1100 ft.	2	47	0	47		
3		23	11	34		Atmosphere dry	4	56	3	59		
5		50	1	51		and cool	6	33	5	38		
9		39	14	53		Experiments in	8	63	0	63		
11		29	1	30		open	10	61	0	61		
		176	78	254	30.7	Av. family 50 +	12	58	0	58		
							14	79	11	90		
							16	37	35	72		
							18	42	0	42		
							20	42	2	44		
								518	56	574	9.7	Av. family 57.

Summary

No. Exp.	No. Non-winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.	No. Exp.	No. Non-winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.
1913–14 13 fam.	312	503	815	61.7	*Winter* Starved 30–32 hours. Av. family 62.	1913–14 5 fam.	175	53	228	23	*Winter* Av. family 45.
1915 7 fam.	187	1	188		*Summer* Woods Hole Starved 45 hours.	1915 7 fam.	344	3	347		*Summer*
1916 5 fam.	176	78	254	30.7	*Summer* Princeton Starved 60 hours.	1916 10 fam.	518	56	574	9.7	*Summer*
Total 25 fam.	675	582	1257	46.3	Av. fam. 50.2	Total 22 fam.	1037	112	1149	9.7	Av. fam. 52.2

Table IV.

1913–14. *Starved.* Parent winged.						1913–14. *Control.* Parent winged.					
No. Exp.	No. Non-Winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.	No. Exp.	No. Non-winged Offspring.	No. Winged Offspring.	Total Family.	Per Cent. Winged.	Remarks.
Winged A[1] 4....	65	2	67	.3	Starved 30 h.	1......	15	0	15.		
	—	—	—			3......	26	0	26		
	65	2	67			5......	25	4	29		
						7......	28	0	28		
						9......	27	0	27		
							—	—	—		
							121	4	125	3.	Av. family 25.
1914–15. Winged G (5).	29	0	29	0	♀ died young. Starved 45 h.	No. controls					
(6).	15	0	15								
	—		—								
	44		44								
Non-winged— G (2)........	11	8			" "	"					
(8)........	44	16									
(9)........	14	15									
	—	—									
	69	29	98	29.							

removed from the plants as soon as it was possible to determine the presence or absence of wing buds.

It has been suggested that young produced in the early part of the reproductive life of the mother would be better nourished and fewer wings would develop than among those born at the end of the period of reproduction. A consideration of the A1 and A2 series of Table I. seems to disprove this, as more wings developed in the families of the older members.

It might also be suggested that the effect of starvation was to reduce the size of the families and consequently the percentage of winged forms might be raised. In some cases the size of families of the starved mothers was smaller than that of the control, in other cases it was greater. The average sized family was 50.2 in the starved lines and 52.2 in the controls. The difference is not large enough to be important.

A few experiments were carried on with starved winged mothers. These are difficult to obtain, since the number normally produced is low and since it is impossible to distinguish wing buds at the early period when starvation is begun, thus the chances for finding winged forms among the starved young are slight. The control experiments (Table IV.), show that of the young of five winged mothers only 3 per cent. were winged. In the few families of starved winged mothers the percentage is less, often none of the young develop wings In passing it might be noted that in the G series (Table IV.) no. 5 and no. 6 winged individuals starved 45 hours produced no winged young, while their wingless sisters nos. 2, 8, 9, produced 29 per cent. winged forms. Apparently starvation has little effect on winged mothers. Teleologically this result would be expected. There would be no need for more winged forms in nature, since the parent had migrated to a fresh food supply.

In conclusion it seems most probable that the lessening of the food supply is the primary factor in determining the development of wings in the offspring of wingless mothers. The wing anlage appears to be present in all the parthenogenetic females and depends directly upon the condition of the food supply of the mother for its stimulation or suppression of development.

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